

NESTING BEHAVIOR OF *TACHYSPHEX LAEVIFRONS* AND
T. CRASSIFORMIS, WITH A NOTE ON *T. KROMBEINI*
(HYMENOPTERA: SPHECIDAE)

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Abstract.—Aspects of the nesting behavior of *Tachysphex laevifrons*, *T. crassiformis*, and *T. krombeini* were studied as part of a larger study on the comparative behavior of species in the *Tachysphex pompiliformis* group. *Tachysphex laevifrons* nested in sand and had only a single, vernal emergence of adults per year. Females did not level the tumulus, left the entrance open while hunting and provisioning, and placed one or two paralyzed *Melanoplus* sp. or *M. puer* group in a short, shallow, single-celled nest. The acridids were small to relatively large in size and transported to the nest in flight or on the ground, respectively. Larger wasps laid larger eggs. Females of *T. crassiformis* exhibited similar behavior, except that they placed from one relatively large *Chortophaga* sp. (North Carolina), *Trimerotropis* sp. (Oklahoma), or *Psinidia fenestralis* (Florida) to four small *Trimerotropis* sp. (Oklahoma) in a one-celled nest in sand. This species of wasp demonstrated seasonal variation in nest dimensions and acridid size and an inverse relationship between prey size and the number of prey per cell. Both *T. crassiformis* and *T. krombeini* were apparently multivoltine in Florida. *T. laevifrons* and *T. crassiformis* affixed their egg on an acridid in a position typical of most other species in the genus. The nesting behavior and ecology of *T. laevifrons* are compared with those of the closely related *T. tarsatus*, while the nesting behavior and ecology of *T. crassiformis* and *T. krombeini* are compared with those of a related species, *T. antennatus*.

Species in the large *Tachysphex pompiliformis* group can be arranged sequentially, using adult external morphology (W. J. Pulawski, pers. comm.). They can also be placed arbitrarily in subgroups using comparative nesting behavior (Kurczewski, 1987), but some behavioral patterns transcend subgroup distinctions. For example, *T. texanus* (Cresson) and *T. psammobius* (Kohl), two totally unrelated species, fly with prey and store several or many, small or tiny acridids, respectively, in a one-celled nest (Kurczewski, 1987). *T. ashmeadii* Fox, *T. montanus* (Cresson), *T. pauxillus* Fox, *T. pompiliformis* (Panzer), and *T. tarsatus*

(Say), species belonging to at least two subgroups, usually carry their prey on the ground, often ventral side up, leave the entrance open during provisioning, and store one or a few, relatively large nymphal, rarely adult, acridids in a single-celled nest (Peckham and Peckham, 1900, 1905; Williams, 1914; Newton, 1956; Evans, 1970; Alcock, 1973; Alcock and Gamboa, 1975; Elliott and Kurczewski, 1985; Pulawski, pers. comm.). On the other hand, certain behavior and prey type can be used to delimit some subgroups. *T. aethiops* (Cresson), *T. punctifrons* (Fox), and *T. pompiliformis* in Europe carry their prey on the ground, dor-

sal side up, and build multicellular nests (Adlerz, 1903; Evans, 1970, 1973; Pulawski, 1971; Alcock, 1973; Kurczewski, 1987; M. F. O'Brien, pers. comm.). *T. pechumani* Krombein is distinctive in its temporary closure of the entrance and leveling of the tumulus (Kurczewski and Elliott, 1978). *T. semirufus* (Cresson) provisions its nests with nymphal Tettigoniidae (Kurczewski and Evans, 1986; Pulawski, pers. comm.).

Information on the nesting behaviors of Nearctic species of the pompiliformis group is fragmentary, consisting mostly of isolated prey records and observations of single females and their nests (Kurczewski, 1987). Only *T. ashmeadii*, *T. pechumani*, *T. pompiliformis*, and *T. tarsatus* have been studied in any detail (Kurczewski and Elliott, 1978; Krombein, 1979; Elliott and Kurczewski, 1985). The following observations on various aspects of the nesting behavior of *T. laevifrons* (Smith), *T. crassiformis* Viereck, and *T. krombeini* Kurczewski are presented to elucidate their phylogenetic relationships within this large and diverse group. The wasp and prey specimens from the study have been given ethology note numbers and deposited in the State University of New York College of Environmental Science and Forestry and Cornell University insect collections, respectively.

Essentially nothing is known about the nesting behavior of *T. laevifrons* (Krombein, 1979). *T. crassiformis* has been studied briefly by Williams (1914) as *T. plenculiformis* Williams and by Krombein (1963) as *T. boharti* Krombein. One female of *T. krombeini* has been observed nesting by Kurczewski (1971).

Williams (1914) noted a female of *T. crassiformis* in Kansas flying with a small acridid. She successively took five small grasshoppers directly into an open nest at intervals of 4–10 min and then closed the burrow with sand, apparently using the forelegs and end of the abdomen. The nest was one-celled, $1\frac{1}{2}$ inches long, and $1\frac{1}{2}$ inches deep which seems unusually vertical for a

species of *Tachysphex*. The cell contained six paralyzed, nymphal tryxaline acridids.

Krombein (1963) presented information on two nests of *T. crassiformis*, one dug by him in North Carolina and the other dug by H. E. Evans in Florida. Krombein observed prey transport of a nymphal acridid slightly larger than the wasp both on the ground and in short flights. The nest he excavated was single-celled, 5 cm deep, and held three nymphal *Psinidia fenestralis* (Serville), each 6–7 mm long. The paralyzed grasshoppers exhibited movements of the legs and palpi. The wasp's egg was placed transversely on the sternum of one prey, near a forecoxa. Evans' observation was of a relatively large acridid carried slowly on the ground by the bases of its antennae and held venter up and head forward. This prey was placed inside the wasp's entrance, pulled into the nest from within, and, 1.5 min after entry, the wasp began filling the burrow with sand. The burrow was 3 cm long and led to a cell, 1 cm deep, which held a single, paralyzed nymph of *Scirtetica marmorata picta* Scudder. The wasp's egg was attached to the "throat" of the prey.

The female of *T. krombeini* observed by Kurczewski (1971) left the entrance open and brought five small prey to her nest in 65 min. The individuals were carried in rather high, rapid flights and held beneath the wasp's body with the legs and mandibles. The female released each prey in the entrance, entered, turned around inside, and pulled in the acridid by its antennae with the mandibles. After the full complement of prey had been placed inside the nest, the wasp filled the burrow with sand, using the forelegs and abdomen. The burrow entered the sand obliquely for 4.8 cm, including cell length, and ended in a small cell, 2.8 cm beneath the surface, including cell height. The cell contained six nymphal acridids (*Melanoplus* sp.) and one nymphal tettigoniid (*Odontoxiphidium apterum* Morse), most of them head inward and ventral side up. The wasp's egg was attached to the left

forecoxal corium of the largest acridid in the cell and extended transversely between the bases of the fore- and midlegs.

Tachysphex laevifrons (Smith)

T. laevifrons has only a single, vernal emergence of adults per year (Kurczewski, 1971). Thirteen females (TX-15) were observed nesting on the sand flats along the Peace River at Arcadia, De Soto County, Florida (see Krombein and Kurczewski, 1963, Fig. 4) during March 25–April 4, 1963, March 26–27, 1965, April 9–10, 1971, and March 29–30, 1972. Females nested in flat, loose, moist, white sand containing decumbent legumes and slopes of bare, white, coarse-grained, firm sand. The nests of three wasps were 11–24 m apart.

Females dug nests, hunted, and provisioned on clear, sunny days at ambient (shade) temperatures of 29°–33°C. During periods of cloud cover, they stopped hunting and rested or cleaned. Females were observed hunting as early as 0925 and as late as 1730 h (EST).

A female searching for a place to dig walked rapidly forward on the sand, moving in a zigzag manner. She held the wings flat on the dorsum when walking and periodically made a rapid flight of several centimeters or, rarely, a few meters to a new area to resume searching. Such a wasp tapped her antennal tips alternately on the sand, sampled the sand with the mandibles, but then usually moved elsewhere. Two females of *T. laevifrons* made false starts 10 and 30 cm apart, respectively. Another wasp made eight trial digs, averaging 4 mm in length, before completing a burrow. One female attempted three burrows in shallow depressions, entered a hole, 5 mm deep, dug laterally, and then also abandoned this excavation.

After breaking the sand crust with the mandibles, the female used the forelegs in unison to rake the loosened sand backward. The body, especially the abdomen, lifted up and down with the digging forelegs. The mid-

and hindlegs were used only for walking in the burrow and entrance and on the tumulus. At intervals the wasp backed out of her excavation and removed sand that had accumulated in the burrow and entrance. The intervals, as measured by the time the female was inside her nest, increased as she dug deeper. One wasp spent only 7–26 s (mean, 13.6) inside between each of her first five sand removals but 10–54 s (mean, 29.0) between individual sand removals 21–25. The female spent 3–8 s (mean, 4.6) working in the entrance and on the tumulus during sand removals 1–5 but only 1–4 s (mean, 2.0) during removals 21–25. She backed onto the tumulus to distances of 0.4–1.8 cm (mean, 1.1; $N = 25$) from the bottom of the entrance in mostly straight or slightly curved directions but made no attempt to level the mound of accumulated sand. The tumuli in front of 10 entrances measured 2.5–4.4 cm (mean, 3.3) long and 2.1–3.0 cm (mean, 2.5) wide.

Females also dug short, shallow burrows in which they rested during rain and spent the night. A wasp exhibited the same components for digging this burrow as she did when she dug a burrow and cell to contain prey. Two females spent 5.5 and 6 min, respectively, to dig a resting burrow. A wasp rested at the end of the burrow, facing the entrance, after closing the opening with sand from inside. One wasp placed a prey in her nest without ovipositing and then dug a resting burrow. She returned to the nest the following morning and finished provisioning it.

A female never closed her entrance while hunting or provisioning. After digging a burrow, she appeared headfirst in the entrance, ran around the opening, and then went off hunting in low rapid flights interspersed with running. Females sometimes hunted small prey on the stems and leaves of plants as far as 25 m from their entrances. Usually, however, a wasp hunted larger prey on the ground or prostrate vegetation within 5–10 m of the entrance. One such female

returned to her nest without prey six times and, each time, entered her burrow, turned around inside in 10–14 s, and exited headfirst. Other hunting wasps did not enter their nests upon returning empty-handed.

Some hunting females pounced on the dorsum of acridids noticeably larger than themselves only to fly off immediately and resume hunting elsewhere. One wasp, weighing (wet) 17 mg, encountered an acridid about twice her size (13.5 mm long) but much heavier (89 mg). After a brief struggle, she managed to turn the grasshopper onto its back but did not attempt to sting it. The acridid righted itself, leapt 1 cm onto a shrub, reared forward, and raised both hindlegs in a threatening manner. The wasp paused, faced the grasshopper, moved her head from side to side, and then went off hunting. Another wasp, weighing 14 mg, stung an acridid weighing only 4.5 mg, abandoned it on the sand, and then stung and abandoned a second acridid weighing 28 mg.

Females always captured and stung prey on the ground. One wasp stung an acridid, weighing only 7 mg, twice in the venter of the thorax and another, weighing 93 mg, five times near the leg bases. A sting insertion averaged 11.3 s (2–20; $N = 7$). Paralysis of the prey still allowed rhythmic movements of the mouthparts, especially palpi, antennae, and abdominal segments.

After stinging, sometimes malaxating the prey with the mandibles, and cleaning herself, a female straddled the acridid head forward and often ventral side up but occasionally on the side or dorsum up. The wasp grasped the prey's antennae with the mandibles and, holding the sides of the grasshopper's body with the hindlegs, proceeded forward on the ground or, in the case of smaller prey, grasped the prey's body with the legs and flew. Manner of transport was related to the relative weights of the wasp and prey: (1) ground, ratio of weight of prey to wasp, $R = 1.9$ – $5.8:1$, mean, 3.3, $N = 7$; (2) 2–15 cm-long flights, 1.2:1, $N = 1$; and,

(3) 1–20 m-long flights, $R = 0.4$ – $0.6:1$, mean, 0.5, $N = 2$. One female with prey 2.1 times heavier than herself moved nearly 1 m in 4 s. A wasp with prey 5.8 times heavier than herself grasped the grasshopper far out on its antennae and, with her hindlegs, near the bases of its forelegs. She had great difficulty in transporting this prey and had to pause frequently. Another female overran her entrance and located it only after making several circles.

Upon reaching the open nest, a female placed the prey ventral side up or on its side with the head just inside the entrance ($N = 8$) or ran directly inside holding the acridid underneath ($N = 2$). The size of the prey usually determined the manner in which it was taken into the nest. However, one acridid the same size as the wasp (weight ratio, 1.2:1) was taken in directly and a smaller prey (0.6:1) was released with its head, thorax, and first three abdominal segments inside the entrance. The wasp entered the burrow, turned around inside, and, using her mandibles, pulled in the prey by its antennae. Wasps brought successive prey to their nests in 3–150 min (mean, 68.6; $N = 5$).

After placing the full complement of prey in a cell and laying an egg on one of the acridids, the wasp filled the burrow and entrance with sand. Females ($N = 5$) appeared headfirst in their entrances 5–6 min after taking in the last prey for the cell and raked sand backward into their burrows, using the forelegs in unison. During this behavior the abdomen moved synchronously up and down and the wings were held flat on the dorsum. As the wasp backed in with sand, her abdomen vibrated rapidly back and forth to pack the sand in the burrow. The mid- and hindlegs were braced against the lower sides of the burrow. When the burrow was filled flush to the surface the wasp moved her abdomen from side to side, smoothing over the fill. One female averaged 21.3 s ($R = 10$ – 40) between her first five trips to the surface to obtain sand but only 8.7 s ($R = 5$ – 15) for the next five trips. She took



Fig. 1. Incomplete nest of *Tachysphex laevifrons* with burrow and cell containing paralyzed, nymphal *Melanoplus* sp.

12 min from entering with her last prey for the cell to filling the burrow flush with the sand surface.

The entrances to 10 nests of *T. laevifrons* were 0.4–0.6 cm (mean, 0.5) in diameter. The burrows penetrated the sand at angles of 30°–38° with the horizon and proceeded obliquely downward to the cell in an almost straight line (Fig. 1). Ten burrows averaged 5.3 cm (4.3–6.6) long, including cell length, and terminated in individual cells at a mean depth of 3.4 cm (2.4–4.2), including cell height. The cells averaged 0.58 cm (0.5–0.7) high, 0.63 cm (0.5–0.7) wide, and 1.20 cm (0.8–1.5) long.

Wasps preyed on the nymphal acridids *Melanoplus* sp. (12 records) and *M. puer* group (4). The number of prey placed in fully-provisioned cells was one or two (mean, 1.6; N = 10). The individual wasps weighed (wet) 11–24 mg (mean, 16.6; N = 8), where-

as their prey averaged 40.8 mg (7–93; N = 16) in wet body weight. The full complement of prey in a cell averaged 67.0 mg (35–137; N = 10).

The acridids were placed in the cells head inward and ventral side up and, in the case of two prey in a cell, laid side by side. In six fully-provisioned cells each with two prey, the egg was attached to the largest and heaviest acridid in the cell. These grasshoppers averaged 49.2 mg (28–76) in wet body weight. In two cells containing individually marked prey, the egg was affixed to the second acridid taken into the nest.

An egg of *T. laevifrons* was sausage-shaped, white, curved slightly, and tapered at the proximal end. It was affixed to a grasshopper by the less tapered, distal end at a forecoxal corium and extended transversely between the first two pairs of legs. Seven eggs were affixed to the prey's left forecoxal

coria and three to the right forecoxal coria. The size of an egg was related to the size of the wasp. Wasps weighing (wet) 12, 14, 23, and 24 mg laid eggs measuring $0.17 \times .040$, $0.18 \times .045$, $0.23 \times .050$, and $0.24 \times .055$ cm, respectively.

Tachysphex crassiformis Viereck

There were two or more flight periods of *T. crassiformis* per year in Florida with dates of collection ranging from March through September. Twenty-nine females were observed nesting in loose sand behind the beaches along the Atlantic Ocean at Fort Pierce Beach, St. Lucie County, Florida on July 16, 1962, April 3, 1963, and March 30, 1965 (TX-8) and at Kill Devil Hills, Dare County, North Carolina on July 23–24, 1962 (TX-9); in the sand flats adjacent to the Peace River at Arcadia, De Soto County, Florida on June 30–July 10, 1962, March 23, 1963, April 6, 1966, April 9–10, 1971, and March 28–April 9, 1973 (TX-12); in a sandy fire-trail at the Archbold Biological Station, Highlands County, Florida on April 12, 1973 (TX-83); and, on the sandy flood plain along the Cimarron River, near Guthrie, Logan County, Oklahoma on July 27 and August 12, 1965 (TX-68, 70). Eight of 22 nests were situated beneath prostrate vegetation, overhanging twigs, or near the bases of grass clumps. Nine entrances were located 1.8–55 m apart.

Females in Florida began nesting in March–April at 0925 h (EST) and nesting activity was at its height at about 1400 on sunny or partly sunny days when the ambient temperature in the shade reached 28°–33°C. No wasp hunted, dug, or provisioned below 27°C. The latest observation (daily) was made at 1534 h.

A female searching for a place to dig exhibited behavior similar to that of *T. laevifrons* (see above), except the velocity of the movements was more rapid. The wasps usually made one or more trial digs before

completing a burrow. One such false start was 5 mm long. Most excavations were begun from the sand surface but one wasp (TX-8) started in a depression 5 mm deep.

The manner in which the burrow was dug was similar to that of *T. laevifrons*, except the digging movements of *T. crassiformis* were noticeably faster. One female (TX-12) paused every 5–10 s and made a hovering flight of 1–2 s, 10 cm above the entrance, until a depth of 3 mm had been reached. These flights were probably in response to high sand surface temperatures (58°–59°C). Another wasp (TX-12) removed sand from the burrow 26 times, remaining inside 21–50 s (mean, 35.5) between successive sand removals. This female, when removing sand, backed further from the entrance at the beginning of the excavation (2–3 cm) than at the end (1–2 cm). A third wasp (TX-68) removed 27 sand loads from the burrow and entrance, stayed outside only 4–27 s (mean, 11.4) per sand removal, rebacked (Kurzewski, 1968) 1–12 times (mean, 4.9) on the tumulus during some of the sand removals, and raked the sand to distances of 0.8–2.2 cm (mean, 1.6) from the entrance. Her times and distances remained approximately the same throughout the excavation. Most wasps walked backward with the sand loads in a straight or nearly straight line and made little attempt to level the tumulus. The tumuli of 15 nests averaged 3.3 cm (2.0–4.5) long, 2.8 cm (1.7–4.0) wide, and 0.5 cm (0.3–0.6) high. The largest tumulus in Florida, 4.5 cm long, 3.0 cm wide, and 0.6 cm high, was associated with the longest burrow (6.0 cm) and second deepest cell (3.1 cm). One female (TX-12) took 12.5 min while another (TX-68) spent 53 min to construct a burrow and cell.

After digging a burrow and cell, a female appeared headfirst in the entrance with the wings held flat on the dorsum. Some wasps (TX-8, 9, 12) then tapped their antennal tips alternately on the tumuli, made four or five runs around an entrance, probably a form

of orientation, and went off hunting in short, low, rapid flights interspersed with running. Other wasps (TX-68) exited headfirst, made 7–13 s long orientation flights, facing the entrances, turned 180° in flight, and flew off. Some females, after exiting and running around the entrances, re-entered their nest one or a few times and backed out of the entrance removing sand with the forelegs. A nest entrance remained open during hunting and provisioning.

Females hunted on the ground or low vegetation, often within 10 m of their entrances. Six wasps (TX-12, 70) captured prey only 0.6–2.1 m from the openings. Wasps ($N = 27$) unsuccessful in capturing prey returned to their entrances 1–5 times, entered their burrows, turned around inside, exited headfirst in 8–50 s (mean, 13), and ran or flew away rapidly. Four females, after entry, removed 1–4 loads of sand from the burrow. Consecutive returns to the nests without prey averaged 18.6 min (2–55; $N = 27$).

A hunting female's antennal movements, running, pivoting, and zigzagging increased in rapidity when in close proximity (5–10 cm) to a potential prey. If the grasshopper remained motionless, the hunting wasp often passed it by. One female (TX-8) increased the rapidity of her searching movements when she ran across an area of sand where a nymphal acridid had been resting 30 s earlier. Some wasps, which encountered acridid nymphs weighing 25–30 mg, touched them with their antennae or flew onto their dorsum, and then flew away. One female (TX-8), weighing 8.5 mg, approached an acridid nymph, 10.5 mm long and weighing 36 mg, mounted it, turned it onto its back, stung it in the right side of the thorax near a hindleg for 14 s, dismounted, and cleaned herself. The grasshopper immediately righted itself and jumped away. The wasp did not follow. She then passed by an acridid nymph, 13 mm long and weighing 84 mg, which raised both hindlegs simultaneously and kicked them backwards. The wasp flew

away immediately. Another female (TX-8) was kicked by the hindlegs of a 15-mm long acridid. She flew a short distance, landed, rested for a few seconds, and cleaned.

Females always stung their prey on the ground, the acridid being on its venter, dorsum or side (Fig. 2). The female bent her abdomen underneath the grasshopper until the apex touched the prey's thoracic venter, presumably the corium surrounding a hindcoxa, and inserted the sting therein. This critical insertion probably prevented the grasshopper from leaping away (Steiner, 1976). The wasp maintained herself dorsum up while attempting to position the longitudinal axis of her body at nearly a 90° angle to that of her prey during subsequent stings in the sequence.

From one to five stings were administered to a single prey during a period of 8–120 s. Whether this represented a partial or complete stinging sequence is unknown (Steiner, 1976). Small prey subsided almost immediately after one or two stings, but more than two stings were necessary to subdue larger grasshoppers. A sting insertion averaged 13.8 s (5–30; $N = 16$). In 12 of 17 stinging sequences, females alternated one or more times between stinging the prey in the left and right sides. Prey were stung into a state of incomplete paralysis which permitted periodic movements of the mouthparts, especially maxillary and labial palpi, and antennae. The abdominal segments exhibited rhythmic breathing movements.

Following the initial sting or, between subsequent stings, the wasp cleaned herself while straddling the prey or, more often, dismounted, walked a few centimeters, and cleaned. This behavior lasted 5–40 s (mean, 11.7; $N = 13$) and consisted of running the antennae through the strigilis and rubbing the hindtarsi over the wings and abdominal apex. One female, after stinging her prey, dismounted, cleaned herself for 15 s, remounted the grasshopper, and malaxated its left forecoxal corium with her mandibles



(Fig. 3). She then turned 180°, cleaned the prey's left hindleg for 75 s, turned back, and malaxated the prey's left forecoxal corium for 26 s. During transport to the nest, she intermittently cleaned and repeatedly malaxated the acridid. Despite this extensive malaxation, the prey was not used for oviposition.

After stinging and malaxating the acridid and cleaning herself, a female straddled the prey usually ventral side up or, rarely, dorsal side up or on the side and head forward. The wasp grasped both antennae of the prey if venter or dorsum up, or one antenna, if on the side, with the mandibles. She then either proceeded forward on the ground, clutching the grasshopper with the hindlegs while using the fore- and midlegs for walking (Fig. 4) or grasped the acridid with the legs and flew. The manner of transport was dependent upon the relative sizes (weights) of the wasps and their prey: (1) ground, ratio of weight of prey to wasp, $R = 2.2\text{--}6.8:1$, mean, 4.4, $N = 12$; (2) 1–4 cm-high and 3–20 cm-long flights, $R = 1.3\text{--}2.3:1$, mean, 1.9, $N = 6$; and, (3) 10+ cm high, 1+ m long flights, $R = 0.3\text{--}1.1:1$, mean, 0.7, $N = 11$. Females varied their position on the prey and the location of the grasp of its body depending upon the acridid's size and weight. Females atop larger (heavier) prey straddled the acridid more anteriorly in order to increase leverage and provide space for the moving fore- and midlegs (Fig. 4). The heaviest prey ($R = 4.2\text{--}6.8:1$, mean, 4.9, $N = 4$) were grasped with the mandibles by their antennae about one-third of the way from the ends or farther out and clutched with the wasp's hindtarsi near the throat or the bases of the forelegs. Medium-sized prey ($R = 1.9\text{--}3.3:1$, mean, 2.5, $N = 8$) were grasped by their antennae about midway

out and with the wasp's hindtarsi near the bases of the midlegs. If a female had difficulty in ground transport such as ascending an incline or slipping on loose sand, she invariably adjusted her position on the prey further anteriorly. One wasp (TX-70) with prey 6.8 times her weight went 0.5 m in 1.5 min, 0.4 m in 1.5 min, and 0.2 m in 47 s, with several second-long pauses in between. The smallest (lightest) prey ($R = 0.3\text{--}1.1:1$, mean, 0.7, $N = 11$) were grasped with the mandibles near the bases of their antennae and, during flight, around the body with the legs.

Upon reaching the nest a female placed an acridid venter up or on its side, rarely dorsum up, with the head and, sometimes, thorax and abdomen just inside the entrance (Figs. 5, 6), or, ran or flew directly inside, holding the grasshopper underneath (Fig. 7). The size and weight of the prey often influenced the manner in which it was taken into a nest: (1) head outside entrance, ratio, 6.8:1, $N = 1$; (2) head inside entrance, $R = 0.6\text{--}5.7:1$, mean, 2.2, $N = 9$; (3) head and thorax inside entrance, 2.1:1, $N = 1$; (4) head, thorax, and abdomen inside entrance, $R = 0.3\text{--}1.1:1$, mean, 0.7, $N = 5$; and, (5) direct entry with prey, $R = 1.6\text{--}1.9:1$, mean, 1.8, $N = 3$. After releasing the prey, entering, and turning around inside the nest, a female appeared headfirst in the entrance in 4–6 s (mean, 5; $N = 5$), and, with the mandibles, pulled the acridid inside by its antennae. The wasp exited in 8–13 s (mean, 11; $N = 7$) if she went in search of additional prey; otherwise, she stayed inside the nest and oviposited. Females brought successive prey to their nests in 3–68 min (mean, 20.3; $N = 11$).

After laying an egg on a prey in the cell, a female filled her burrow with sand. Wasps

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Figs. 2–4. 2, Female of *Tachysphex crassiformis* inserting sting near base of right hindcoxa of nymphal *Psinidia fenestralis*. 3, Female of *Tachysphex crassiformis* malaxating left forecoxal corium of recently stung, nymphal *Psinidia fenestralis*. 4, Female of *Tachysphex crassiformis* transporting nymphal *Psinidia fenestralis*, holding grasshopper's antennae with mandibles and body with hindlegs.



came out of their entrances headfirst to obtain sand 2–7.5 min (mean, 3.8, $N = 6$) after entering with their last prey. The components of filling in the nest were essentially as described under *T. laevifrons*, except the movements of *T. crassiformis* were more rapid. Three females (TX-8) came out of their entrances as far as 2.5–3.0 cm every 5–35 s to obtain loose sand for the fill, whereas four others (TX-68) went only 0.4–1.3 cm every 1–2 s. Two wasps (TX-8, 70) came out to get sand 14 and 9 times, respectively, to complete the fill.

After filling the burrow nearly flush with the surrounding sand, some females turned 180° every several seconds and tapped their antennae on the fill. They then turned back and, standing on the filled entrance with the mid- and hindlegs spread and, curving the abdomen underneath, vigorously hammered the fill. Five females (TX-8, 12, 70) took from 5 to 14 min (mean, 7.1; $N = 5$) to fill their burrows and entrances flush with the surrounding sand.

Females of *T. crassiformis* dug short, shallow burrows which entered the sand obliquely at angles of less than 45° to the surface and terminated in single cells. Burrow length and cell depth dimensions from Florida, North Carolina, and Oklahoma are presented in Table I. The seasonal differences in mean burrow length and cell depth from Florida and North Carolina nests are highly significant (t (length) = 3.660; $df = 13$; $\alpha < 0.01$; t (depth) = 5.883; $df = 13$; $\alpha < 0.001$). Similarly, mean burrow length and cell depth from July and August Oklahoma nests are significantly different (t (length) = 11.446; $df = 4$; $\alpha < 0.001$; t (depth) = 18.807; $df = 4$; $\alpha < 0.001$). Entrance diameters averaged 0.43 cm ($R = 0.3$ – 0.8 ; $N = 15$), the burrow diameters

being only slightly smaller ($R = 0.3$ – 0.5 cm; mean, 0.35). Fourteen March–April cells from Florida were 0.5–0.7 cm (mean, 0.61) high, 0.6–0.7 cm (mean, 0.66) wide, and 1.0–1.2 cm (mean, 1.09) long. In Oklahoma four cells from July were 0.5–0.6 cm (mean, 0.53) high, 0.5–0.6 cm (mean, 0.58) wide, and 0.9–1.0 cm (mean, 0.98) long, whereas two cells from August were 0.7 cm high, 0.8 cm wide, and 1.5–1.6 cm long. The Oklahoma cell differences correlated positively with the use of four small prey per cell in July and one or two much larger individuals per cell in August.

Females preyed on the nymphal acridids *Chortophaga* sp. in North Carolina (1 record), *Psinidia fenestralis* (Serville) in Florida (20), and, *Trimerotropis* sp. in Oklahoma (17), all members of the subfamily Oedipodinae. The number of prey stored in fully-provisioned March–April Florida cells ranged from 1 to 4 (mean, 2.5; $N = 12$) but was only 1 in Florida and North Carolina cells during July ($N = 3$). These mean differences are highly significant ($t = 4.313$; $df = 13$; $\alpha < 0.001$). In Oklahoma in July females stocked four cells each with four prey but used only one or two (mean, 1.5; $N = 2$) acridids per cell in August ($t = 5.774$; $df = 4$; $\alpha < 0.01$). Regardless of locality the number of prey per cell was inversely related to the sizes (weights) of the individuals: one prey per cell, 21–84 mg (mean, 45.4; $N = 5$); two prey, 11–81 mg (mean, 24.6; $N = 14$); three prey, 11–35 mg (mean, 18.9; $N = 12$); and, four prey, 2–22 mg (mean, 8.3; $N = 20$). Prey individuals from Florida (March–April) were significantly heavier than those from Oklahoma (July) ($t = 5.1227$; $df = 47$; $\alpha < 0.0005$) but significantly lighter than those from Oklahoma (August) ($t = 3.2087$; $df = 33$; $\alpha < 0.0025$).

←
 Figs. 5–7. 5, Female of *Tachysphex crassiformis* releasing relatively large nymph of *Psinidia fenestralis*, ventral side up, in entrance. 6, Abdomen and legs of relatively large, nymphal *Psinidia fenestralis* projecting from entrance after its release. 7, Female of *Tachysphex crassiformis* entering nest with relatively small nymph of *Psinidia fenestralis*.

Table 1. Seasonal variation in nest dimensions of *Tachysphex crassiformis*.

Locality	N	Range	Mean \pm SD
Burrow Length (cm)			
Florida, March–April	12	3.8–6.0	$4.9 \pm 0.72^{***}$
Florida–North Carolina, July	3	3.0–3.7	$3.3 \pm 0.36^{***}$
Oklahoma, July	4	6.6–7.6	$7.3 \pm 0.47^{***}$
Oklahoma, August	2	2.8–3.2	$3.0 \pm 0.30^{***}$
Cell Depth (cm)			
Florida, March–April	12	1.9–3.5	$2.8 \pm 0.45^{***}$
Florida–North Carolina, July	3	1.0–1.4	$1.2 \pm 0.20^{***}$
Oklahoma, July	4	4.3–4.7	$4.4 \pm 0.19^{***}$
Oklahoma, August	2	1.1–1.4	$1.3 \pm 0.21^{***}$

*** Data within brackets are statistically significant at 99% confidence level.

Prey from Oklahoma (August) were significantly heavier than prey from Oklahoma (July) ($t = 5.625$; $df = 18$; $\alpha < 0.0005$). The mean sum weights of the prey per cell were: one prey per cell, 45.4 mg ($R = 21-84$; $N = 5$); two prey, 49.2 mg ($R = 30-92$; $N = 7$); three prey, 56.7 mg ($R = 45-72$; $N = 4$); and, four prey, 33.2 mg ($R = 16-65$; $N = 5$). Tests (t) applied to all pairwise combinations of the means are not significantly different at $\alpha = .05$. Female wasps from Florida weighed 5–14 mg (mean, 9.1; $N = 11$), whereas wasps from Oklahoma weighed 6–10 mg (mean, 7.6; $N = 5$). These mean differences are not significant ($t = 0.985$; $df = 14$; $\alpha > 0.20$).

In 18 fully-provisioned cells containing from 1 to 4 prey per cell, all acridids were positioned ventral side up and head inward. In four other cells (TX-8, 68), each with four prey, one acridid was placed dorsum up and head inward and three were placed venter up and head inward. In all 22 cells the acridid bearing the wasp's egg was positioned ventral side up and head inward. In six of the cells, each with two prey placed side by side, the egg was attached to either the left or right acridid equally. In one cell with two acridids laid in tandem, the egg was placed on the prey that was farthest in. In each of four cells with one acridid piled atop

another, the egg was placed on the uppermost prey. The egg was affixed to the heaviest acridid in 12 of 16 cells with two or more prey, an intermediate-sized prey once, and the lightest prey three times. In one cell with two acridids (TX-70) the egg was affixed to a prey weighing only 9 mg while the other grasshopper weighed 68 mg.

The mean weight of an egg-bearing prey of *T. crassiformis* was 26.7 mg (7–84; $N = 18$) while other prey individuals in the cells averaged only 15.7 mg (2–68; $N = 35$), a significant difference ($t = 2.269$; $df = 51$; $\alpha < 0.05$). In nine examples of two or more prey per cell eggs were laid on the initial acridid taken into the nest (3), second prey taken in (2), or last grasshopper taken in (4). Two egg-bearing acridids had received extensive malaxation by the wasps, whereas three other extensively malaxated acridids were not oviposited upon.

An egg of *T. crassiformis* was similar to that of *T. laevifrons* except for being smaller in size. Eight such eggs (TX-8, 9, 12, 68) averaged 0.16 (0.15–0.18) cm long and 0.042 (0.040–0.045) cm wide at the middle. The egg was placed similarly to that of *T. laevifrons* but fit more tightly into a depression on the underside of the thorax of the oedipodine prey. Although certain females affixed their eggs consistently to the left (TX-

68) or right (TX-12, 70) sides of their prey, the sum of the affixation sites was 11 to the left and 10 to the right forecoxal corium.

Tachysphex krombeini Kurczewski

One female was observed searching for a place to dig a burrow on the sand flats beside the Peace River at Arcadia, Florida on April 10, 1973. She walked rapidly in a zigzag pattern and finally selected a depression in bare sand. She began digging with the mandibles and then removed the loosened sand backward, using the forelegs in unison. She held the wings flat on the dorsum. The movements of her forelegs were rapid and her forward and backward movements within the entrance were noticeably jerky. The female did not attempt to level the small mound of sand that accumulated in front of the entrance. After 4.5 min of digging, the wasp turned 180°, filled the entrance with sand, using the forelegs in unison, and flew away, abandoning the excavation.

DISCUSSION

Tachysphex laevifrons is similar morphologically and behaviorally to *T. tarsatus*. The latter species occurs commonly throughout much of the United States and southern Canada but only sparingly in the Southeast, being absent entirely from southern Georgia and Florida (Pulawski, pers. comm.). *T. laevifrons* is essentially a geographic replacement of *T. tarsatus*, inhabiting not only southeastern U.S. but also extending rarely into Texas, Oklahoma and Kansas (Krombein, 1979; Pulawski, pers. comm.). Whereas *T. tarsatus* has two flight periods per year in northeastern U.S. and more than two at southern latitudes, *T. laevifrons* has only a single, vernal flight per year (Kurczewski, 1971). In this regard the latter species resembles *T. pechumani* (Kurczewski and Elliott, 1978).

Females of both *T. laevifrons* and *T. tarsatus* occur in sparsely vegetated sandy soil, often constructing nests near the bases of

plants. The components involved in searching for a nesting site and burrow construction are essentially identical. Both species make little attempt to level the tumulus, run around the entrance for orientation prior to hunting, leave the entrance open during hunting and provisioning, and hunt in proximity to their nests. *T. laevifrons* and *T. tarsatus* capture medium-sized or relatively large, occasionally small, usually nymphal acridids, transport them on the ground or in low flights, depending on their size and weight, take them into the entrance variously, based on their size, and store one or a few paralyzed individuals in a single-celled nest. Final closure of the nest contains essentially identical components in the two species. The nests of *T. laevifrons* and *T. tarsatus* are short and shallow with an oblique burrow. Prey of both species are placed in the cell mostly head inward and ventral side up and the wasp's egg is affixed to a forecoxal corium of the acridid, extending transversely between the bases of the fore- and midlegs. The acridids captured by *T. tarsatus* comprise members of three subfamilies (Williams, 1914; Krombein, 1979; Elliott and Kurczewski, 1985), whereas those caught by *T. laevifrons* consist only of species of *Melanoplus*. The apparent narrow prey preference of the latter species may be related to its having been studied at only a single locality in Florida.

T. crassiformis, *T. krombeini*, and *T. antennatus* are allied morphologically and behaviorally. *T. crassiformis* has an extensive distribution throughout North, Central, and South America (Krombein, 1979). *T. antennatus* also occurs throughout much of the U.S. and Mexico but is replaced in southeastern U.S. by *T. krombeini* (Pulawski, pers. comm.). *T. crassiformis* and *T. krombeini* nest in areas of sand inhabited also by *T. laevifrons*. *T. antennatus* inhabits abandoned gravel pits and gravelly paths along the edges of woodlands (pers. observ.). None of the three species nest in ag-

gregations and, consequently, the entrances of conspecific nests are often widely scattered. Based upon dates of collection *T. crassiformis* and *T. krombeini* have two or more generations per year in Florida (Kurczewski, 1971), while *T. antennatus* has only a single generation per year with a small, partial second generation during optimal summers (Pulawski, pers. comm.; pers. observ.).

In searching for a nesting site and digging a nest *T. crassiformis*, *T. krombeini*, and *T. antennatus* exhibit rapid movements. Those of a *T. krombeini* or *T. antennatus* female digging within her entrance are sometimes rather jerky and include much rebacking, as in *Plenoculus davisii* (Fox) (Kurczewski, 1968) and *Diploplectron peglowi* Krombein (Kurczewski, 1972). Williams (1914) noted the same behavior for digging females of *T. crassiformis* (as *T. plenoculiformis*) in Kansas. However, I found the digging movements of *T. crassiformis* to resemble those of *T. tarsatus* (Williams, 1914) and *T. ashmeadii* (Elliott and Kurczewski, 1985). During digging neither *T. crassiformis*, *T. krombeini*, nor *T. antennatus* level the sand that accumulates in front of their entrances.

Females of all three species omit a temporary closure of the entrance during hunting and provisioning. *T. crassiformis* and *T. antennatus* capture medium-sized or small acridid nymphs which they carry to their nests in low flights (Williams, 1914; Elliott and Kurczewski, 1985), but the former species also preys upon relatively large acridid nymphs which are transported on the ground (Krombein, 1963). There is a relationship between prey size, method of transport, and manner of entry into the nest in *T. crassiformis* and *T. antennatus*. Relatively large prey are invariably carried close to the ground, released with their head inside the entrance and pulled into the nest from within, whereas small prey are often flown directly into the entrance. There is seasonal variation in prey storage related to prey size in *T. crassiformis* (see also Wil-

liams, 1914; Krombein, 1963). *T. krombeini* provisions with small prey, carries them in extensive flights, and stores several individuals in a cell, after releasing each one with its head in the entrance during entry (Kurczewski, 1971).

Final closure of the nest in all three species involves raking sand backward into the tunnel with the forelegs which are bent medially and packing the sand into place with the apex of the abdomen (Williams, 1914; Kurczewski, 1971, pers. observ.). The movements exhibited during this behavior are very rapid.

T. crassiformis and *T. krombeini* dig rather straight, short burrows which enter the sand obliquely and terminate in single cells (Williams, 1914; Krombein, 1963; Kurczewski, 1971). With few exceptions (Krombein, 1963), seasonal variation in burrow length and cell depth is evident in *T. crassiformis*. In contrast *T. antennatus* digs a short, curving, single-celled nest, often beneath a flat stone, and demonstrates only slight variation in nest dimensions (pers. observ.).

The majority of prey of *T. crassiformis*, *T. krombeini*, and *T. antennatus* is placed in cells head inward and venter up, and the wasp egg is laid on an individual so positioned. The egg is affixed as in *T. laevifrons*, except that of *T. crassiformis* fits tightly against the thoracic sternum of oedipodine prey. Whereas *T. krombeini* stores both nymphal acridids and tettigoniids in the cell (Kurczewski, 1971), *T. crassiformis* and *T. antennatus* provision only with nymphal acridids. Both *T. krombeini* and *T. antennatus* capture a preponderance of *Melanoplus* spp. (Cyrtacanthacridinae) (Kurczewski, 1971; Elliott and Kurczewski, 1985; pers. observ.), whereas *T. crassiformis* preys upon Oedipodinae (Krombein, 1963; pers. observ.) and Tryxalinae (Williams, 1914).

In conclusion, the morphology and nesting behavior of *T. laevifrons* and *T. tarsatus* are alike. No single behavioral characteristic can be used to separate the two species.

The single, annual spring appearance of *T. laevifrons* adults and the restriction of this species essentially to southeastern U.S. provide allochronic and geographic evidence for its distinctness. *T. tarsatus* is multivoltine at southern latitudes and occurs throughout the U.S. except for southern Georgia and Florida. Although *T. crassiformis*, *T. krombeini*, and *T. antennatus* are morphologically similar, *T. krombeini* can be separated readily from the two other species by its use of tiny acridid and tettigoniid prey and its extensive provisioning flights. *T. antennatus* nests in gravelly soil beneath stones and stores several *Melanoplus* spp. (Cyrtacanthacridinae) in a cell, whereas *T. crassiformis* nests in sandy soil beneath vegetation or in the open and places one or a few Oedipodinae, rarely several Tryxalinae, in a cell. *T. crassiformis* exhibits much variation in nesting behavior throughout its range.

ACKNOWLEDGMENTS

I thank K. V. Krombein, Smithsonian Institution, and M. G. Spofford, SUNY-CESF, for reviewing the manuscript and assistance with statistical tests, respectively, and M. F. O'Brien, The University of Michigan, for permitting me to examine his unpublished manuscript on the nesting behavior of *Tachysphex aethiops*. I am indebted to K. V. Krombein and W. J. Pulawski, California Academy of Sciences, for confirming the identities of the species of *Tachysphex*, and, A. B. Gurney (retired), Systematic Entomology Laboratory, BBII, Agricultural Research Service, USDA, for identifying the prey Acrididae. W. J. Pulawski kindly permitted me to examine his unpublished manuscript on the *Tachysphex* of North and Central America. I am grateful to the late Richard Archbold for providing the excellent facilities of the Archbold Biological Station, Lake Placid, Florida, which was used as a base for many of the studies. I especially thank N. F. R. Snyder, Portal, Arizona for the photographs used in the text. Sigma Xi

RESA Grants-in-Aid of Research provided partial funding for this study during 1962, 1963, and 1966.

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